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MUTATION *EN MASSE*

HARLEY HARRIS BARTLETT¹

DURING the writer's experiments with *Oenothera* two different species have been discovered of which certain strains give rise by mutation to large numbers of dwarfs. In both cases the dwarfs occur in far greater numbers than experience would lead one to expect, even in the most actively mutant strain. Similar, although not exactly parallel, phenomena have been observed by both de Vries and Davis in certain hybrid *Oenotheras*, but not, as far as the writer knows, in any unhybridized species. Since the cultures have now been continued long enough so that there can be no doubt as to the accuracy of the observations, the least complicated of the two cases is here placed on record. It concerns *Oenothera Reynoldsii* sp. nov. (A technical diagnosis of this species will be published elsewhere.) The seeds from which the cultivated strain arose were collected at Knoxville, Tennessee, in the fall of 1910, by Dr. E. S. Reynolds, then connected with the botanical department of the University of Tennessee.

Fig. 1 is a diagram showing the size and relationship of the cultures of *Oenothera Reynoldsii* which have thus far been grown. No diversity was found in the small F_1 and F_2 cultures, of only ten and five plants, respectively, which were grown in 1911 and 1912. The F_3 generation of twenty-six plants, grown in 1913, exhibited

¹ From the Bureau of Plant Industry, U. S. Department of Agriculture, Office of Plant Physiological and Fermentation Investigations. Published by the permission of the Secretary of Agriculture.

a most unexpected segregation into three marked types, *forma typica*, reproducing the parental form, and two dwarf types, *mut. semialta* and *mut. debilis*, so named because of their resemblance to the two classes of dwarfs which de Vries² obtained from *E. nanella* \times *E. biennis*. *Mut. semialta* is about half as tall as *f. typica* and has a

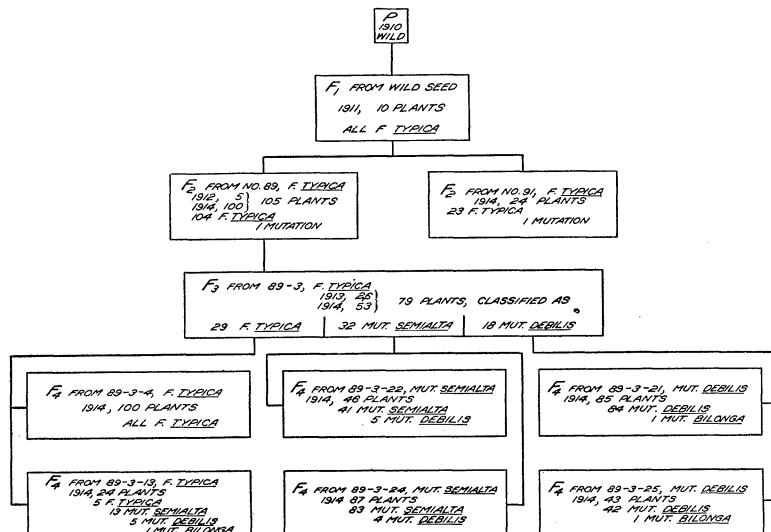


FIG. 1. Diagram showing the size and relationship of the cultures of *Ono-thera Reynoldsii*, 1911-1914.

very dense and showy inflorescence in which the fruits and flowers are very little smaller than in the parent form. The leaves, however, are decidedly reduced. *Mut. debilis* is more variable in size than *mut. semialta*, but averages about half as high as the latter. Its fruits and flowers are somewhat reduced, but by no means proportionately to the size of the plant. The leaves, on the contrary, are much more reduced than those of *mut. semialta*. The inflorescence is not as dense, but often longer.

The unlooked-for occurrence of these types in the *F*₃ of 1913 led to the duplication in 1914 of both the *F*₂ and *F*₃ generations from seeds which had been left over from former years. In 100 additional *F*₂ plants of the mutant

² "Gruppenweise Artbildung," pp. 241-244.

strain there were 99 plants of *f. typica* and one mutation of a quite different type from either *mut. semialta* or *mut. debilis*. The original F_3 culture had consisted of 26 plants, including two of *f. typica*, 16 of *mut. semialta*

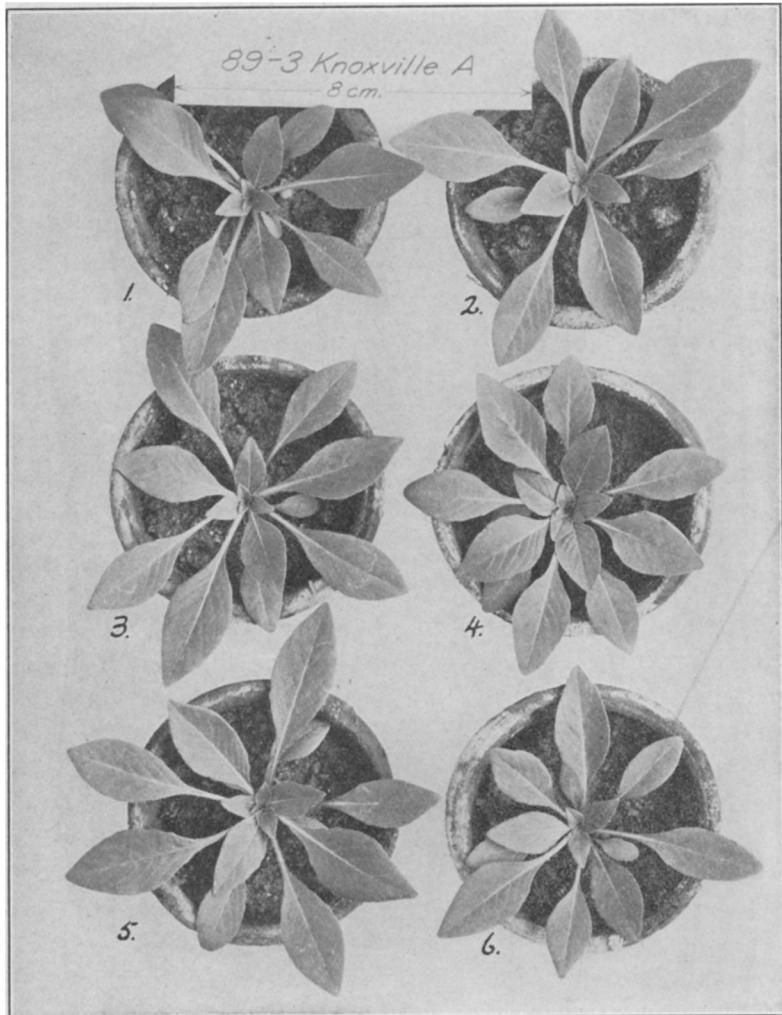


FIG. 2. A random sample of six plants from the F_3 culture of 1913. No. 4 is *f. typica*; the rest are all *mut. semialta*.

and eight of *mut. debilis*. In the supplementary culture of 53 sister-plants, grown in 1914, there were 27 plants of *f. typica*, 16 of *mut. semialta* and ten of *mut. debilis*.



FIG. 3. Adjacent plants of *mut. debilis* (on the left No. 89-3-25, chosen as parent of one of the F_4 progenies) and *mut. semialta* (on the right; No. 89-3-24, chosen as parent of one of the F_4 progenies). The small labels on the plants are 10 cm. long. (Reduction same as in Fig. 4.)

There can therefore be no doubt that the F_2 was an essentially uniform generation and that the F_3 was the first generation to throw the two dwarf types, except perhaps as rare mutations, which were not detected on account of the small size of the cultures. In this connection it may be remarked that the mutations of *Oenothera Reynoldsii* can not be detected in very young cultures with any degree of precision. Up to the time the rosettes are set out in the garden, after they have been started in the greenhouse in pots, they show no consistent differences among themselves. It happens that six seedlings of the 1913 F_3 were photographed before any diversity whatever had been detected in the culture. They must therefore be considered a random sample from the 26 plants. All turned out to be *mut. semialta* except one, which was *f. typica*. The photograph is reproduced as Fig. 2.

At maturity the contrast between the classes is very

striking, and leaves no room for doubt as to the proper classification of any individual. Fig. 3 shows adjacent plants of *mut. debilis* and *mut. semialta*; Fig. 4 *mut. debilis* and *f. typica*. Figs. 5, 6 and 7 show branches of the three forms, on the same scale of reduction.

The F_4 generation, grown in 1914, consisted of the progenies of two plants of each of the three types. The two externally identical parent plants of *f. typica* (there



FIG. 4. Adjacent plants of *mut. debilis* (in front) and *f. typica* (behind; No. 89-3-13, chosen as parent of one of the F_4 progenies). The small labels on the plants are 10 cm. long. (Reduction same as in Fig. 3.)

were only two in the F_3 of 1913) proved to be of very different genetic constitution. The progeny of one, numbering 100 plants, were all strictly like the parent, showing not the slightest deviation from *f. typica*. The other progeny, however, repeated the diversity of the F_3 generation, containing five plants of *f. typica*, 13 of *mut. semialta* and five of *mut. debilis* in a culture of 24 plants. This progeny, also, included one plant of a third dwarf

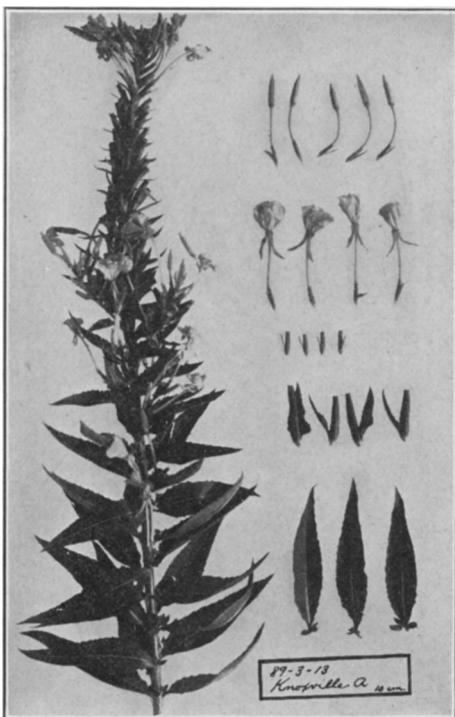


FIG. 5. *Enothera Reynoldsii* *f. typica*. Branch from F_3 plant No. 89-3-13, chosen as parent of one of the F_4 cultures. The entire plant is shown in Fig. 4.

mutation, which will be referred to below as *mut. bilonga*.

The two F_3 plants of *mut. semialta* which were used as parents gave very similar progenies, consisting of *mut. semialta* and *mut. debilis*. In one case the numbers were 41 of *mut. semialta* and five of *mut. debilis* in a total of 46; in the other case, 83 of *semialta* and four of *mut. debilis* in a total of 87.

The two progenies from *mut. debilis* parents, containing 85 and 43 plants, respectively, were all *mut. debilis* like the parents, except that each progeny contained one individual of *mut. bilonga*. Before discussing the latter mutation it may be well to capitulate.

1. The individuals of *f. typica* are of two kinds, (a) those which do not throw dwarfs, and (b) those which throw from 60 per cent. to 80 per cent. of dwarfs.

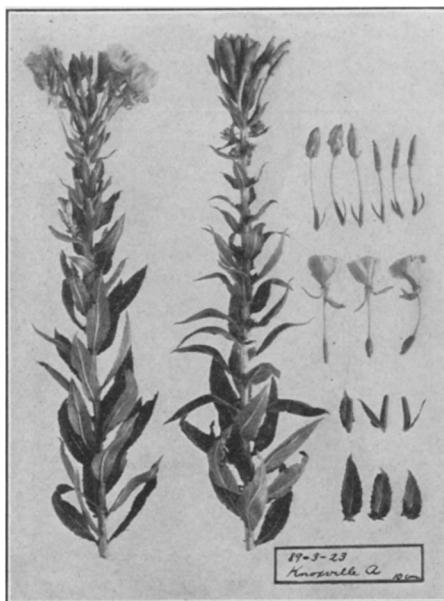


FIG. 6. *Mut. semialta*. Branches of F_3 plant No. 89-3-23.

2. The dwarfs are of two kinds, one of which, *mut. semialta*, is intermediate between *f. typica* and the extreme dwarf, *mut. debilis*.

3. *Mut. semialta* reproduces itself in the greater part of its progeny, but throws a small number (seemingly about 7 per cent.) of *mut. debilis*.

4. *Mut. debilis* does not throw either *f. typica* or *f. semialta*. It comes true, except for the fact that it rarely throws *mut. bilonga*.

Mut. bilonga is by far the most interesting of the variants of *Oenothera Reynoldsii*. It has occurred once as a

primary mutation from *f. typica*, and twice as a secondary mutation from *mut. debilis*. Although *mut. debilis* seems to be an extreme recessive, derived from *f. typica* either by the simultaneous or by the successive loss of two factors for height, it throws *mut. bilonga*, which shows a return to the stature of *mut. semialta*. In fact, *mut. bilonga* would be identical with *mut. semialta* if it were not for the difference in the length of the fruits. It has already been stated that in both *mut. semialta* and *mut. debilis* the fruits are by no means as reduced in size as the foliage and stems. It seems almost as though the

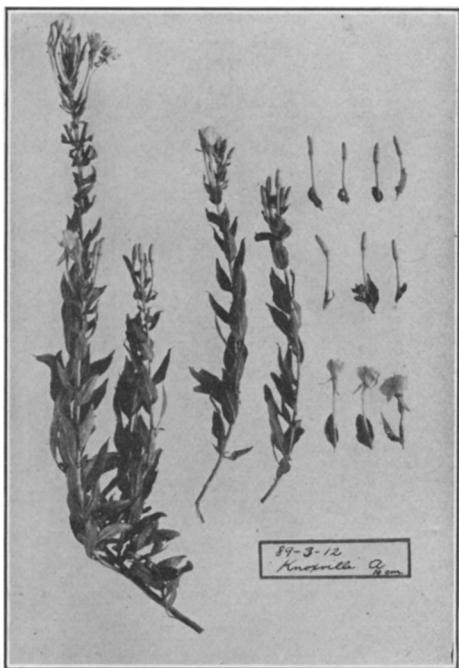


FIG. 7. *Mut. debilis*. Branches of F_2 plant No. 89-3-12. The entire plant is shown in Fig. 4.

process of mutation, which results in the formation of either of these dwarfs, does not involve the factors determining fruit size. In other words, the slight reduction in size seems not to be due to a modification of the hereditary qualities of the plant, but rather to diminished nutrition. If this explanation is the true one, the fruits of *mut.*

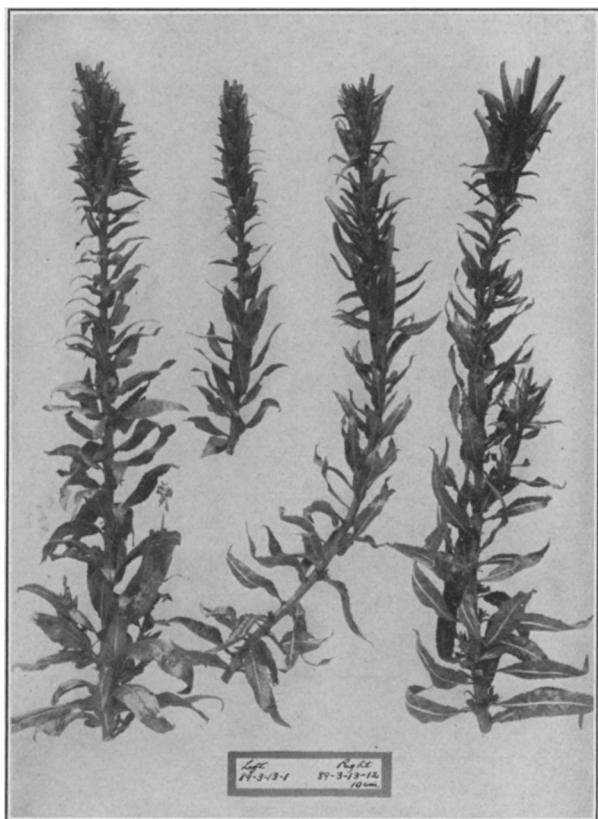


FIG. 8. Branches of mut. *semialta* (left; No. 89-3-13-1) and mut. *bilonga* (right; No. 89-3-13-12) showing the similarity of the foliage and dissimilarity of the fruits, which are twice as long in the latter as in the former. The two mutations were sister-plants in the progeny of an F_3 f. *typica*; No. 89-3-13, shown in Figs. 4 and 5.

debilis are small for the same reason that the late autumn fruits on weak lateral branches of f. *typica* are small. When, by mutation to mut. *bilonga*, mut. *debilis* reassumes the stature and foliage size of mut. *semialta*, there is a modification of the characters which determine the length of the fruit. Not only is the stature doubled, and the length of the leaves doubled, but the length of the fruit is also doubled. Mut. *bilonga* is to all outward appearance the same as mut. *semialta*, except that the fruits are twice as long. Thus, we have the anomalous situation that mut. *bilonga*, a dwarf type, is characterized by the

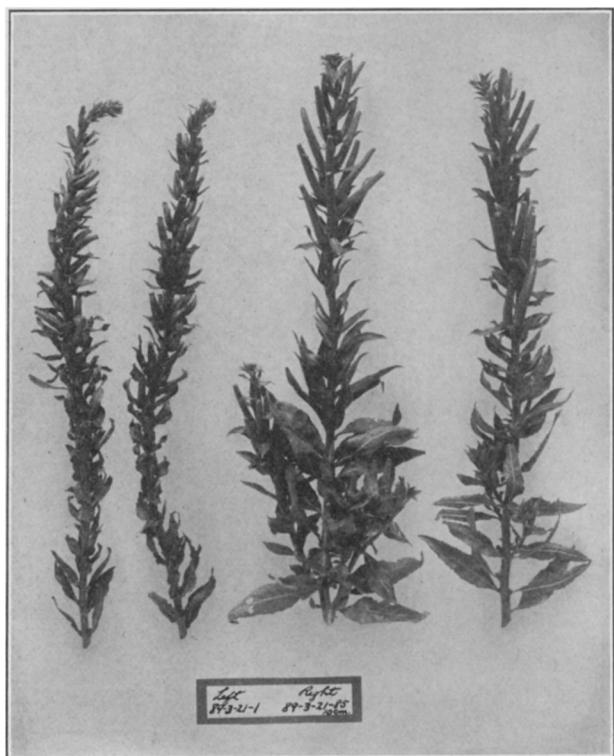


FIG. 9. Branches of mut. *debilis* (left; No. 89-3-21-1) and mut. *bilonga* (right; No. 89-3-21-85) showing dissimilarity in both foliage and fruits. The two forms were sisters in the progeny of one of the original examples of mut. *debilis* which appeared in the F₃ of 1913.

longest fruits in the subgenus *Onagra*. Exceptional fruits are 70 mm. long; the average length of six hand-pollinated fruits was 62 mm. By way of comparison, it may be stated that the length of the average fruit of f. *typica* is about 33 mm., and that the longest is 38 mm. None of the immediate allies of *Oenothera biennis* have longer fruits than those of *O. Reynoldsii* f. *typica*, although there are allies of *O. muricata* in which the fruits average as long or longer. There is no species, however, in which the fruit length of mut. *bilonga* is even approached. Here we have an apparent case of progressive mutation, which will be tested out as soon as possible. Mut. *bilonga* has not thus far been carried into a second generation. Both it and the two other dwarfs are completely self-fertile,

and furnish an abundance of good seed. It is planned to make a biometrical study of fruit length next year, when the second generation of mut. *bilonga* will be available.

In Fig. 8 the two branches on the left are mut. *semialta*; the two on the right mut. *bilonga*. The plants which furnished the material belonged to an F_4 culture from *f. typica*, containing five plants of *f. typica*, 13 of mut. *semialta*, five of mut. *debilis* and one of mut. *bilonga*. In Fig. 9, on the contrary, the contrast is between sister-plants of mut. *debilis* and mut. *bilonga* in the progeny of mut. *debilis*. A comparison of the figures will show the identity of mut. *bilonga* from the two sources.

The phenomenon presented by *Oenothera Reynoldsii*, called mutation *en masse* for want of a better name, seems of sufficient interest to justify this preliminary paper. The fact that it appears in one of the short-styled, self-pollinating species makes it of especial interest. An explanation can hardly be attempted until the interrelationships of the various derivations have been worked out by a series of crosses. Nevertheless, it seems clear that mutation *en masse* bears a certain degree of resemblance to Mendelian segregation. The fundamental mutation which causes the diversity possibly occurs in only one of the two gametes in a generation preceding the one in which diversity becomes manifest. It is masked by the dominance of the parental characters transmitted through the other gamete. Segregation then occurs in the following generation. No explanation suggests itself for the enormous surplus of dwarfs in the progenies exhibiting diversity, unless perhaps it is that the results are complicated by selective germination or selective mortality. At any rate, the ratios thus far obtained do not conform to any Mendelian expectation. Larger cultures, to be grown next year, may prove more enlightening.

To the mutationist, the most interesting problem presented by *Oenothera Reynoldsii* is the origin of mut. *bilonga* from mut. *debilis*, involving, as now seems probable, the origin of a new character.